

DIET-INDUCED AND MORPHOLOGICAL COLOR CHANGES IN JUVENILE CRAB SPIDERS (ARANEAE, THOMISIDAE)

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ABSTRACT. The effect of dietary pigments on abdominal color of juvenile spiders was examined in the laboratory using the flower-dwelling crab spiders *Misumenops asperatus* (Hentz 1847), *Misumenoides formosipes* (Walckenaer 1837), and *Misumena vatia* (Clerck 1757) (Thomisidae). Because these species lack hypodermal chromes, ingested prey pigments may show through the epidermis and affect opisthosomal coloration. Diet-induced color changes were restricted to the opisthosoma, and all three spider species responded similarly to dietary pigments. Opisthosomas of instars 2–4 fed red-eyed fruit flies turned pink, and the pink color faded back to the normal white over a period of 4–6 days. Opisthosomas of instars 5–7 fed red-eyed fruit flies remained white, as did opisthosomas of all instars fed white-eyed fruit flies (controls). In a field population of *M. asperatus*, 82% of spiders in July (instar 2), 93% of spiders in August (instars 3–4), and 8% of spiders in September (instar 5) had pink, orange, or brown opisthosomas. Yellow juveniles were also seen: 5% and 57% of *M. asperatus* observed in August and September, respectively, were yellow. Yellow juvenile *M. formosipes* were observed in the field as well. The yellow color did not result from dietary pigments, but was, rather, a morphological color change and included the prosoma and limbs, as well as the opisthosoma.

Keywords: Flower spiders, opisthosoma, prey pigments, size-dependent effect

The ability of certain species within the family Thomisidae (crab spiders) to undergo a reversible color change depending on their environmental substrate, a process referred to as a morphological color change (Holl 1987), has provoked interest among naturalists since the late nineteenth century (Angus 1882; Packard 1905; Gadeau de Kerville 1907; Gabritschevsky 1927; Gertsch 1939; Weigel 1941). Most investigations of morphological color changes among thomisids have focused on the goldenrod spider, *Misumena vatia* (Clerck 1757) (e.g., Packard 1905; Gabritschevsky 1927; Millot 1926; Weigel 1941), and the ability to change color has been attributed only to adult females (Gabritschevsky 1927).

Misumena vatia is typically white, but turns yellow when placed on a yellow substrate. Because this species lacks hypodermal chromes and has a translucent cuticle, reflection of white light from guanine crystals in the intestinal diverticula causes *M. vatia* to appear

white (Millot 1926; Weigel 1941). Under the stimulus of reflected yellow light (Gabritschevsky 1927; Weigel 1941), a yellow pigment is released into the hypoderm (Weigel 1941), and the yellow color becomes more intense the longer a spider remains on a yellow substrate (Packard 1905; pers. obs.). Morphological color changes involve a spider's entire body: prosoma, opisthosoma, and limbs take on a yellow hue. Similar morphological color changes have been reported in other thomisid species, including *Misumenoides formosipes* (Walckenaer 1837) and *Misumenops asperatus* (Hentz 1847) (Gertsch 1939; Schmalhofer 1996).

Having a colorless, translucent integument has an interesting side-effect on juvenile flower-dwelling crab spiders: ingested material that is strongly pigmented may show through the epidermis, changing the color of a spiderling's opisthosoma. In the field, juvenile crab spiders having pink, orange, brown, green, yellow, or white opisthosomas have been observed (Schmalhofer 1996). Peck & Whitcomb (1968) observed similar diet-induced color changes in the clubionid *Cheiracanthium inclusum* (Hentz 1847), a pale yellow

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spider with a transparent integument. They noted that spiders turned green and pink when fed pyralid larvae and red-eyed *Drosophila*, respectively; and they obtained a variety of opisthosomal colors by feeding spiders an artificial diet containing dye (Peck & Whitcomb 1968). No information was provided, however, concerning how long color changes lasted, their frequency of occurrence under natural conditions, or the instars affected. Using flower-dwelling crab spiders, I performed a laboratory experiment to determine the duration of diet-induced color changes and the instars affected. Field observations were also conducted to determine the frequency of occurrence of diet-induced color changes in a natural crab spider population.

METHODS

Effects of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders.—

The effect of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders was examined using *M. asperatus*, *M. formosipes*, and *M. vatia*. Adults of the three species are seasonally separated. *Misumenops asperatus* matures and females lay a single egg sac in spring, and spiderlings emerge in early summer and overwinter as late instar juveniles (pers. obs.). *Misumenoides formosipes* matures in midsummer, females produce a single egg sac in late summer or early autumn, and spiderlings generally overwinter in the egg sac (pers. obs.). *Misumena vatia* matures and females produce a single egg sac in early-to-midsummer, and spiderlings emerge in late summer and overwinter as middle-instar juveniles (Fritz & Morse 1985). These species have seven juvenile instars, the first of which is spent in the egg sac (Gertsch 1939).

Misumenops asperatus and *M. formosipes* were reared from egg sacs produced by females collected in Middlesex and Somerset Counties, New Jersey. Adult specimens of *M. asperatus* and *M. formosipes* have been deposited at the American Museum of Natural History. I have never found *M. vatia* in New Jersey, although the species is recorded as occurring in the state (Gertsch 1939). *Misumena vatia* used in the laboratory experiment originated in Lincoln County, Maine, and egg sacs were provided by D. Morse. Egg sacs were maintained at room ambient temperature (25–30 °C); and, after emergence, second instar

spiderlings were placed in separate 4 dram shell vials with cotton plugs. Spiders were starved for seven days prior to a feeding trial to ensure that their guts were empty (Anderson 1970; Nakamura 1987). During a feeding trial, a spider was supplied with either 10 red-eyed fruit flies (experimental group) or 10 white-eyed fruit flies (control group). Any flies not consumed after five hours were removed. After feeding, a spider's opisthosomal color was subjectively categorized as bright pink, moderately pink, pale pink, or white. The number of days required for a spider's opisthosoma to return to the normal white color was also noted. This protocol was repeated during each juvenile instar (instars 2–7) for each species. The number of spiders used in a feeding trial varied with species and instar ($n = 6$ –20).

Natural occurrence of juvenile *Misumenops asperatus* having colored opisthosomas.—

Field observations focused on *M. asperatus* and took place in a 2.8 ha² field adjacent to the Busch campus of Rutgers University in Middlesex County, New Jersey. I tagged 250 inflorescences each of *Achillea millefolium* (yarrow), *Daucus carota* (Queen Anne's lace), and *Solidago* spp. (goldenrod), which were plant species commonly used by *M. asperatus* (Schmalhofer 1996). *Solidago* was the dominant plant species in the field, occupying approximately 76% of the area and having a density of 55.4 stems per m². *Achillea* patches were interspersed among the *Solidago* and covered approximately 6% of the area. *Achillea* had a density of 31.7 stems per m². *Daucus*, with a density of 16.6 stems per m², occurred at the field perimeter and covered approximately 14% of the area. Blooming in *Achillea*, *Daucus*, and *Solidago* occurred sequentially over the course of the summer, and flowering phenology in the three species showed little overlap (pers. obs.). Flowering in *Achillea* occurred from early June to mid-July, flowering in *Daucus* occurred from mid-July to mid-August, and flowering in *Solidago* occurred from mid-August through September. Over seven consecutive days at the beginning of July, August, and September, I made daily surveys of tagged *Achillea*, *Daucus*, and *Solidago*, respectively. Observations occurred between 0900–1200 h, and I recorded the number of spiders per inflorescence and spider color.

RESULTS

Effects of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders.—

Misumenops asperatus, *M. formosipes*, and *M. vatia* responded similarly to *Drosophila* eye pigments. When fed red-eyed fruit flies, only a spider's opisthosoma changed color: prosoma and legs were unaffected by dietary pigments. I found that the opisthosomas of instars 2–4 fed red-eyed *Drosophila* turned pink, and the pink color slowly faded to the normal white over a period of 4–6 days. Intensity and duration of the color change varied with age of the spider. Second instar spiders turned bright pink, while older spiders took on a pale-to-moderate shade of pink. Intensity of opisthosomal color in instars 3–4 also seemed to vary with the number of *Drosophila* consumed: spiders capturing a single fly turning pale pink, while those capturing multiple prey (2–3 flies) took on a darker hue. Few spiders captured more than one fly. Opisthosomal color of older instars returned to normal more quickly (4 days) than did that of younger spiders (6 days). Opisthosomal color of instars 5–7 was not affected by *Drosophila* eye-pigments, regardless of the number of flies consumed. Opisthosomas of all spiders in the control groups fed white-eyed *Drosophila* remained white.

Anecdotal observations indicated that the intensity and duration of dietary color changes and instars affected were also influenced by the causative pigment. For instance, the opisthosoma of an instar 5 *M. asperatus* that consumed a blood-fed mosquito turned dark brown, and the color faded over a six-day period. Opisthosomas of instars 4–5 of *M. asperatus* found in the field feeding on unidentified green hemipterans turned brilliant green, but returned to normal after only two days.

In all three species, spider size changed by more than an order of magnitude during the juvenile period. Mass of instar 2 spiders was less than 1 mg, while average mass of instar 7 (penultimate) female spiders was much greater: 48 mg (*M. vatia*, calculated from Fritz & Morse 1985; Morse 1988; Morse & Stephens 1996), 42 mg (*M. formosipes*), and 24 mg (*M. asperatus*).

Natural occurrence of juvenile *Misumenops asperatus* having colored opisthosomas.—The proportion of spiders showing di-

etary color changes was very high in July and August (Table 1), and pink or orange opisthosomas were the most commonly seen variations. The yellow color observed in juvenile *M. asperatus* in August and September was not dietarily induced, but was, rather, a morphological color change like that described for adult spiders (see introduction). The effects of dietarily acquired pigments were restricted to the opisthosoma, but yellow juveniles were fully colored; prosoma and limbs, as well as the opisthosoma, were yellow. Both male and female spiderlings were observed to turn yellow. Juvenile *M. formosipes* also proved capable of undergoing a morphological color change; 8% of juveniles seen in July (instars 5–6) and 50% of juvenile females seen in August (instar 7) were yellow. I have also observed yellow *M. formosipes* in sweepnet samples collected earlier in the season (May and June). The seasonal increase in the proportions of yellow juveniles in both *M. asperatus* and *M. formosipes* populations reflected an increase in the availability of plant species with yellow flowers (predominantly *Solidago*) during the course of the summer.

Spider position on inflorescences varied with plant species. On *Achillea*, most *M. asperatus* were found on the underside of inflorescences; on *Daucus*, spiders occurred with similar frequencies on the upper surface and the underside of inflorescences; and on *Solidago*, most spiders wedged themselves between the individual flowers comprising an inflorescence. Having a colored opisthosoma did not appear to influence spider position on inflorescences of any of the plant species examined. This observation, however, was not quantified.

DISCUSSION

Although opisthosomal color provides some clues as to a juvenile crab spider's recent feeding history, opisthosomal color should not be used as a means of categorizing juveniles in field populations as hungry or satiated. Too many variables affect opisthosomal color (e.g., number of prey ingested, spider age, time since ingestion, causative pigment, etc.) to make opisthosomal color a reliable indicator of hunger status. Also, many prey types captured by flower-dwelling crab spiders lack strong pigments and, thus, would not affect spider color.

Table 1.—Proportions of *Misumenops asperatus* of various colors seen during the summer months in central New Jersey. Values presented are averaged over the seven days of observations each month. Spider densities are presented as mean number of spiders per inflorescence (± 1 SD); 250 inflorescences of each plant species were surveyed. Flower color is indicated below each plant species. Spider colors marked with an * are diet-induced.

Month	Plant species	Instar	Spider density	Spider color				
				White	Yellow	Pink*	Orange*	Brown*
July	<i>Achillea millefolium</i> (white)	2	0.09 (0.06)	0.18	0.00	0.82	0.00	0.00
August	<i>Daucus carota</i> (white)	3–4	0.83 (0.11)	0.01	0.05	0.50	0.38	0.05
September	<i>Solidago</i> spp. (yellow)	5	0.07 (0.03)	0.35	0.57	0.01	0.07	0.00

The effect of dietary pigments on flower-dwelling crab spiders appears to be limited by spider size: smaller (younger) juveniles show the effects of prey pigments, while larger (older) juveniles are generally unaffected. Like older juveniles, adult females are unaffected by prey pigments (pers. obs.): mature female spiders fed red-eyed fruit flies *ad libitum* in the laboratory never displayed opisthosomal color changes, nor have I ever observed adult females in the field to be affected by pigments of ingested prey. In contrast to female crab spiders, adult males are small, typically 5 mg or less (Morse & Stephens 1996; pers. obs.). Because adult *M. vatia* and *M. asperatus* males largely lack opisthosomal chromes, abdominal color in males of these species has the potential to be affected by diet. However, this seems to be a rare occurrence. During eight years of field research, I have observed only a single adult male *M. asperatus* showing dietary pigments. The opisthosomal hypoderm of adult male *M. formosipes* contains yellow chromes, which would obscure any ingested pigments. Thus, mature male *M. formosipes* are not subject to diet-induced color changes.

The differential effect of prey pigments on younger vs. older spiders, as seen in the laboratory experiment, can be explained by gut volume and feeding habits. Crab spiders begin feeding from their prey's head (Pollard 1989, 1993; pers. obs.); therefore, eye pigments are ingested early during feeding. Compared to older (larger) spiders, younger (smaller) individuals have correspondingly small gut capacities and their smaller stomach muscles probably exert less force during feeding (this was not tested). Consequently, younger spiders ex-

tract less material from a given prey item than do older spiders, and eye pigments compose a larger fraction of the ingested food. The tendency of crab spiders to discard one prey item before all the available material has been extracted and to begin feeding on a new prey item when prey is abundant (Pollard 1989) may have enhanced the effect of *Drosophila* eye pigments on opisthosomal color of younger juveniles. When offered an abundance of prey, Pollard (1989) found that crab spiders discarded the original prey item after a period of time corresponding to the length of time spent feeding from the head when only one prey item was provided.

Morphological color changes in crab spiders are erroneously described as being restricted to adult female spiders (Gabritschewsky 1927; Gertsch 1939; Hinton 1976; Holl 1987). This assertion is based on Gabritschewsky's (1927) experiments with laboratory-reared *M. vatia*, and does not hold true for *M. asperatus*, *M. formosipes*, or natural populations of *M. vatia*. In the field, juvenile *M. vatia* have been observed to undergo morphological color changes (D. Morse pers. commun.). It is possible that Gabritschewsky's results were due to the restricted diet (*Drosophila*) given to the spiderlings or to some other difference between the laboratory and field environment (e.g., light intensity, substrate character). Light quality or intensity in particular may be important in effecting morphological color changes: compared to color changes occurring under natural conditions, color changes occurring under artificial lighting take longer to complete and a paler yellow hue results (pers. obs.).

The ability to turn yellow has obvious benefits for juvenile (and adult) crab spiders. By enhancing crypsis on yellow flowers, yellow spiders are less likely to be detected by predators or prey. This capability would be particularly useful for juvenile spiders if a large portion of the juvenile period coincided with a seasonal increase in the availability of yellow-flowered plant species, as occurs in *M. asperatus*. Conversely, the impact of dietary color changes on crab spider fitness parameters, such as prey capture success and susceptibility to predators, is unknown, but presumably would be negative. At the study site, most plant species available in early-to-mid-summer had white flowers. Therefore ingested prey pigments could cause a spiderling to contrast strikingly with its floral substrate. However, since pink and orange were the predominant opisthosomal colors, apparency to insects may not have been strongly affected. Most insects are considered to be red-blind (Borror et al. 1989; Barth 1991), but this interpretation of insect visual systems has recently been challenged (Chittka & Waser 1997). Susceptibility to visual predators with good color perception/discrimination, such as birds, could be enhanced by spider ingestion of prey pigments. Further studies are needed to determine what, if any, impact diet-induced color changes have on crab spider fitness parameters.

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